# Accounting for continuous species' responses to management effort enhances cost-effectiveness of conservation decisions

Lorenzo Cattarino[1,2*], Virgilio Hermoso[2,3,4], Lindsay W. Bradford[2], Josie Carwardine[5], Kerrie A. Wilson[6], Mark J. Kennard[2,3] and Simon Linke[2,3]

[1]*MRC Centre for Outbreak Analysis and Modelling, Department of Infectious Disease Epidemiology, Imperial College London, London, United Kingdom*

[2]*Australian Rivers Institute, Griffith University, 170 Kessels Rd, Nathan, Queensland, 4111, Australia*

[3]*National Environmental Research Program Northern Australia Hub, Griffith University, 170 Kessels Rd, Nathan, Queensland, 4111, Australia*

[4]*Centre Tecnologic Forestal de Catalunya. Crta. Sant Llorenc de Monunys, Km 2, 25280 Solsona, Lleida, Spain*

[5]*CSIRO Ecosystem Sciences, Dutton Park, Queensland 4102, Australia*

[6]*School of Biological Sciences, The University of Queensland, St. Lucia, Qld 4072, Australia*

*Corresponding author at: MRC Centre for Outbreak Analysis and Modelling, Department of Infectious Disease Epidemiology, Imperial College London, London, United Kingdom (Tel: +44 (0)20 7594 3229; Email: l.cattarino@imperial.ac.uk)

19 Abstract

20 Limited resources available for conservation require prioritizing location and level of
21 conservation management efforts to abate threats to species. Ideally, the optimal level of
22 management effort to allocate to an action should be informed by the species' responses to
23 actions. This would enhance cost-effectiveness of conservation recommendations. How
24 continuous species responses to varying levels of management effort ('species response
25 curves') affect the cost of abating threats to species is poorly understood, but critical for cost-
26 effective threat management.

27 We developed an optimization approach to prioritize management efforts based on varying
28 species response curves. We tested our framework in the Mitchell River catchment, northern
29 Australia, to find the optimal level of effort to allocate to restoration of river connectivity and
30 riparian revegetation to improve persistence of freshwater fish species. We compared the
31 results of our analysis against a traditional approach, which assumes that (1) an action is
32 either fully implemented or not; and (2) when the action is fully implemented the species
33 persists; when the action is not implemented, the species goes locally extinct.

34 We showed that by using species response curves we can abate threats to species at budgets
35 up to 20% lower than when applying the traditional approach. Our approach can aid
36 identifying how much effort (i.e., area managed, timeframe of management or budget
37 invested) to allocate to multiple actions, and where, to cost-effectively abate threats to
38 species. This has the potential to significantly improve biodiversity outcomes when resources
39 are limited, by improving precision of on-ground conservation decisions.

40 **Keywords**: Spatial conservation prioritization; multi-action planning; priority threat
41 management; ecological responses; freshwater; Australia.

## 1. Introduction

Biodiversity is declining due to a variety of threatening processes and funds for threat management are limited (Butchart et al. 2010; Pimm et al. 2014). Systematic conservation planning can aid in prioritizing the most cost-effective (i.e., greatest conservation outcome achieved per unit cost) management actions to implement, and where, to abate threats to biodiversity (Margules and Pressey 2000). However, the type and location of the most cost-effective priority actions to implement will depend on how species respond to the management actions (Carwardine et al. 2012). Increasing levels of management effort can result in a continuous range of species responses (Martin et al. 2009). Accounting for such 'species response curves' may increase cost-effectiveness of conservation decisions (Adams et al. 2014). While there is a large body of literature on priority threat management (Auerbach et al. 2014; Carwardine et al. 2012; Chades et al. 2015; Wilson et al. 2007), there is little understanding of how integrating information on continuous species responses to management effort into conservation planning, could improve the cost-effectiveness of abating threats to species.

Species response curves describe a continuous relationship between (1) the level of management effort allocated to an action in an area (e.g., extent of area being managed, timeframe of management or budget being invested) and (2) the magnitude of the species outcome (e.g., improved species persistence) (Adams et al. 2014; Wilson et al. 2005). Understanding the shape of species response curves would allow greater precision in allocation of conservation effort, potentially reducing the costs of threat abatement plans. For example, the benefits of controlling invasive species for native fauna increase rapidly as the level of control increases, and then plateau before complete eradication of the pest occurs (Choquenot and Parkes 2001). As a result, the minimum level of effort required to substantially improve persistence of native species is lower than 100%, with consequent

savings in the cost of implementing actions. Use of species response curves for cost-effective allocation of conservation effort has also been suggested in the case of the responses of plant species to restoration of natural fire and hydrological disturbance regimes, and the responses of ecosystem service provision to area of land conserved (Bestelmeyer 2006; Kremen 2005). However, the integration of continuous species response curves into systematic conservation planning has been limited, largely because it is computationally challenging (Adams et al. 2014).

Systematic conservation planning applies the principle of complementarity, which identifies sets of sites for implementing actions that collectively achieve the greatest contribution in terms of protecting native species (Moilanen et al. 2009). Species responses to management effort have typically been represented in conservation planning using a binary approach (Carwardine et al. 2008; Klein et al. 2008; Possingham et al. 2000; Pressey et al. 1994), which is based on two key assumptions: (1) an action is either not implemented, or fully implemented by allocating the highest level of management effort (binary effort); (2) when the action is not implemented the species goes extinct from the local area; when the action is implemented the species persists (binary outcome). Some studies consider the possibility that species have a likelihood of persistence in absence of an action (non-binary outcome), but assume a binary effort (Billionnet 2013; Carwardine et al. 2012; Polasky et al. 2005; Pouzols et al. 2012; Watts et al. 2009). There is currently little understanding of how continuous species responses, which account for both continuous effort and continuous outcome, influence cost-effectiveness of threat management.

The aims of this study are to (i) develop an optimization approach for prioritizing varying levels of effort to remediating actions, accounting for different possible responses of species to the action, and (ii) quantify the effect of the shape of species response curves on the overall cost of abating threats to species. We first demonstrate the efficiency of our

approach relative to a traditional binary approach, using a simulated example. We then apply the approach to a case study in northern Australia, where we prioritize levels of effort to abate two threats to 44 freshwater fish species. We show that by explicitly accounting for species response curves, the overall cost of improving species outcomes can be reduced up to 20%, relative to the cost required when the shape of species responses is ignored. Our approach can increase the cost-effectiveness of threat management in systematic conservation planning. Our findings can guide more precise allocation of on-ground conservation management effort to improve species persistence.

## 2. Materials and methods

### 2.1. Conceptual framework

We developed a conceptual framework to understand how different species responses to actions can affect the overall cost of abating threats to species. The responses represented varying relationships between (1) the probability (ranging from 0 to 1) of persistence of a species in a planning unit and (2) the level of effort allocated to the action that abates the threat.

We considered species, and the threats affecting them, distributed across multiple planning units. Our conservation objective is to improve the probability of persistence of species by prescribing actions that abate the threats. The improvement in a species probability of persistence, following action prescription, depended on the type of species response to the action. A binary species response, with binary effort and binary outcome, assumes that any level of effort below a certain threshold yields a species benefit of 0 and has a cost of 0; any level of effort above the threshold yields a species benefit of 1 and has a cost of 1 (step function, Fig. 1a) (Arponen et al. 2005; Carwardine et al. 2009). As a result, the cost of

implementing an action in a planning unit to abate the threat, and achieving the highest probability of species persistence, corresponds to the cost of prescribing the highest level of effort of the action (Fig. 1c).

Here, we conceptualized species responses as continuous curves where any level of effort could be selected and could have different species benefits, in terms of probability of species persistence (Fig. 1b). We assumed that a species goes extinct from a planning unit if no level of effort was implemented to remediate a threat. However, as opposed to studies which assume a binary species outcome, we allowed a species to have continuous levels of probabilities of persistence following allocation of continuous levels of effort.

We considered species response curves with different shapes (Arponen et al. 2005) (Fig. 1b): (A) 'convex', where the probability of persistence increases quickly, at first, and then plateaus as more effort is applied; (B) 'sigmoid', where the probability of persistence increases slowly and is high only after a certain level of effort is applied; and (C) 'linear', where the probability of persistence increases linearly with the level of effort. The benefit of implementing an action depends on the form of the response curve. For example an effort of 0.8 translates into a higher probability of persistence of a species when assuming a convex or a sigmoidal form than when assuming a linear form (Fig. 1b). The cost of implementing an action in a planning unit to abate a threat depends on the level of effort necessary to achieve a certain probability of persistence for the species (Fig. 1d). For the sake of simplicity, we assumed that the cost of implementing an action in a planning unit is a linear function of the level of management effort allocated to the action (Santika et al. 2015). We then asked the question: how does accounting for different shapes of species response curves affect the overall cost of abating threats to species across multiple planning units?

## 2.2. Prioritization problem

Our aim is to find the optimal level of effort for each action in each planning unit, to ensure representation of all species in a minimum area, at the lowest cost. The minimum area, which represents the conservation objective or *target*, indicates the area, out of the total area of occupancy of a species, where the probability of persistence of the species was 1. Mathematically, our problem can be formulated through the following objective function:

$$\min \sum_{i=1}^{N_p} f_k\left(X_{i,k}\right) \qquad \text{eqn 1}$$

subject to achieving the representation target

$$\sum_{i=1}^{N_p} R_{i,j} > T_j, \quad \text{for all species } j, \qquad \text{eqn 2}$$

where $X_{i,k}$ denotes a control matrix indicating the level of effort selected for action $k$ in planning unit $i$, where $X_{i,k} \in [0,1]$ is the level of effort, which is a uniformly distributed variable between 0 and 1, $i \in \{1, 2, ..., N_p\}$ and $k = \{1, 2, ..., N_a\}$, where $N_p$ and $N_a$ denote the total number of planning units and actions, respectively; $f_k$ is the function to transform the selected level of effort of action $k$ into the cost of implementing action $k$ in planning unit $i$, $R_{i,j}$ is the representation level of species $j$ in planning unit $i$ (see below) achieved through all the selected levels of effort, and $T_j$ is the target level for species $j$, where $j \in \{1, 2, ..., N_s\}$ and $N_s$ is the total number of species.

The probability of persistence of a species, following selection of a particular level of effort of an action, depended on the assumed shape of the species response curve. We assumed that different actions had an additive impact on species representation in a planning unit (i.e., no interaction between the impacts of different actions) (Auerbach et al. 2015). The representation level, $R_{i,j}$, of species $j$ in planning unit $i$ was expressed as follows:

163 $$R_{i,j} = a_{i,j} \times \frac{\sum_{k=1}^{N_a} d_{i,k}[g_{k,j}(X_{i,k})]}{Z_{i,j}} \quad \text{eqn 3}$$

164 where $a_{i,j}$ is the area of occupancy of species $j$ in planning unit $i$, $g_{k,j}$ is the function which
165 transforms the selected level of effort, for each action $k$, into probability of persistence of
166 species $j$ ($g_{k,j}$ represents the shape of the species response), $X_{i,k}$ denotes the control matrix
167 indicating the level of effort selected for action $k$ in planning unit $i$, $d_{i,k} \in \{0,1\}$ is a control
168 variable indicating weather action $k$ is available in site $i$, and $Z_{i,j} = \sum_{k=1}^{N_a} d_{i,k}[g_{k,j}(1)]$ is the
169 sum of the probabilities of persistence of species $j$, achieved by selecting the highest level of
170 effort (i.e., 1) for all actions available in planning unit $i$. Equation 3 scales the area of
171 occupancy of a species in a planning unit by the probability of persistence of the species
172 following implementation of selected available actions. Dividing by $Z_{i,j}$ ensures that the
173 representation level of a species in a planning unit is proportional to the effort required to
174 eliminate completely all threats to the species. If there are two actions available in a planning
175 unit, and only one action is selected with a level of effort of 1, assuming $g_{k,j}$ is a linear
176 function for both actions and the species occupies 10 km$^2$ of the planning unit (i.e., $a_{i,j}$=10),
177 $R_{i,j} = 10 \times \frac{1}{2} = 5$.

178 To ensure the achievement of targets we calculated a species penalty which was a
179 function of the amount of target that had not been met, for each species. The cumulative
180 species penalty, $Sp$, for all species $N_s$ was calculated as follows:

181 $$Sp = \sum_{j=1}^{N_S} SPF_j H(s_j) s_j \quad \text{eqn 4}$$

182 where *SPF* (Species Penalty Factor) is a scaling factor which determines the relative
183 importance of meeting the target for each species. The Species Penalty Factor was set to 10,

184 which was the minimum value to ensure all targets were 100% met. The step function, $H(s_j)$,
185 takes a value of zero when $s_j \leq 0$ and 1 otherwise. The shortfall $s_j$ represents how much of the
186 representation target for each species is not met and is equal to $T_j - \sum_{i=1}^{Np} R_{i,j}$ . Calculating the
187 shortfall jointly over all planning units ($N_p$) ensures that the set of priority planning units and
188 actions collectively provides the greatest contribution in terms of achieving conservation
189 goals (i.e., principle of complementarity) (Margules and Pressey 2000).

190 Since the decision problem described in eqn 1-2 can be too large to solve using
191 techniques guaranteed to find optimal solutions, such as optimal integer programming or
192 stochastic dynamic programming, we used simulated annealing to search for near-optimal
193 solutions. Simulated annealing (Kirkpatrick et al. 1983) works by iteratively introducing
194 random changes in the configuration of selected planning units and actions. Changes are
195 accepted or not based on how they modify a measure of the optimization objective. Good
196 changes are always accepted while bad changes are accepted with a probability which
197 decreases as the annealing proceeds. This technique, similar to the cooling of metals, aids the
198 algorithm to escape non-optimal solutions.

199 We adapted the simulated annealing algorithm described in Cattarino et al (2015). This
200 approach finds a minimum set of actions, and sites where to implement those actions, to
201 completely abate threats to species at the minimum cost, by iteratively adding or removing
202 one action from the solution. We slightly modified the approach of Cattarino et al. (2015) to
203 find the minimum set of levels of effort to allocate to multiple actions and planning units, to
204 abate different threats to species at the lowest cost. A complete description of the simulated
205 annealing algorithm is reported in Appendix S1.
206

207 2.3. Simulated example

208 We demonstrated the effect of different shapes of species response curves on the cost of
209 achieving a species target using a simulated example. We first modelled an artificial
210 landscape as a 50 × 50 cell-based grid, where each cell represents a planning unit. We
211 simulated the spatial distribution of 50 species, each one with a 0.5 Bernoulli-distributed
212 probability of occurring in each planning unit. The actual area of occupancy of each species
213 was randomly drawn from a uniform distribution between 0 and 100. For simplicity, we only
214 considered one threat and assumed that it occurred in all the planning units. We used different
215 forms of the $g_{k,j}$ function to represent different shapes of species response curves (Table 1).
216 To demonstrate the effect of the response shapes, we assumed that in this simulated example
217 all species exhibited the same response shape to the action that remediated the threat. We
218 used relative costs, rather than real monetary values, as we were interested in the relative
219 differences in the costs of achieving targets for species with different response shapes, rather
220 than in absolute values.

221 For each shape of species response curve, we considered 20 different target levels, $T_j$,
222 between 50 and 1,000 km$^2$ with an increment of 50. For example, a target level of 50
223 translates into ensuring a probability of persistence of 1 in 50 km$^2$. For each combination of
224 species responses × target levels (4 × 20 = 80 simulation scenarios), the simulated annealing
225 algorithm was run 10 times for each of the 80 scenarios with 1 million iterations. For each
226 best solution (i.e., the one with the lowest objective function value), we recorded the total
227 cost of the selected levels of effort across all planning units.

228

229 2.4. Case study

230 We tested the cost-effectiveness of our approach, relative to the traditional binary
231 approach, using a case study in the Mitchell River catchment in northern Australia. Our aim

was to prioritize levels of management effort to abate threats to freshwater fish species using real data on the spatial distribution of two threats, two actions and different responses for different species to each action. We delineated 2,316 planning units (hydrologically-defined sub catchments, 30 $km^2$ average area) across the catchment, using ARC Hydro for AcrGIS 9.3 (ESRI 2013). We calculated the area of occupancy of all the freshwater fish species (44 species) occurring in the study area using information from a larger database on aquatic species distributions in northern Australia (Kennard 2010).

We considered two major threats, including (1) presence of dams and weirs, which can represent barriers to fish movements, and (2) grazing land use, which can degrade riparian zones, leading to increased nutrient and sediment loading into rivers and a consequent decrease in aquatic habitat quality (Hermoso et al. 2013; Pusey et al. 2011). We characterized the occurrence of each threat in each planning unit using data on the location and relative size of artificial barriers to movement caused by dams, weirs and other in-stream structures (Stein et al. 2002), and the occurrence of grazing land use (ABARES 2010) as a surrogate for riparian vegetation degradation. Each threat could be abated by a different action: (a) installation of fish passage devices (e.g. fish ladders, locks or lifts) on dams, weirs and other barriers to restore habitat connectivity and (b) fencing of riparian areas to reduce cattle pressure on riparian vegetation.

To quantify the cost-effectiveness of our approach relative to the binary approach, we considered two scenarios: (1) one scenario where all species had the same binary response (i.e., both binary effort and binary outcome) to each of the two actions ('binary' scenario); and (2) one scenario where we used different species response curves for different actions ('continuous-response' scenario). For the continuous-response scenario we defined the response curve of each one of the 44 fish species to each action based on prior reviews (Pusey et al. 2011) and data on species-specific traits that may increase species vulnerability

257 to threats (Pusey et al. 2004; Sternberg and Kennard 2013; Sternberg and Kennard 2014) (See
258 Appendix S2 for details on how species response curves were defined).

259 For each scenario, we considered the effect of varying the target level on the
260 prioritization output. For each target level considered (20 values, see above), the simulated
261 annealing algorithm were run for 1 million iterations and replicated each one 10 times, for a
262 total of 200 runs per scenario. For each best solution, we recorded the total cost of all the
263 selected levels of effort.

264

265 3. Results

266

267 3.1. Effect of the shape of species response curves on the cost of achieving targets

268 Generally, the overall cost of meeting species targets, when assuming convex and
269 sigmoid species responses, was lower than when using a binary response (Fig. 2). The
270 magnitude of the improvement of considering a convex or a sigmoid response depended on
271 the target level. For example, the 100 $km^2$ target for species with a convex response was met
272 at almost half of the cost required when using a binary response. Gains in cost-effectiveness
273 were smaller for species with a sigmoid response. Convex and sigmoid species responses also
274 outperformed the linear response. There was virtually no difference between the costs of
275 achieving targets for species with linear and a binary responses. As the target level increased,
276 the effect of different forms of species responses on the total cost of achieving targets was
277 less pronounced.

278 The level of effort prescribed in all the selected planning units, when using a binary
279 response (Fig. 3a), was the highest. The level of effort prescribed in most of the selected
280 planning units, for a convex and sigmoid response (Fig. 3b and 3c) was lower than for a
281 binary and linear response (Fig. 3a and 3d). In the scenario with a convex response, most of

282 the planning units had either a very low level of effort (around 0.2) or a high level of effort
283 (around 0.7). In the scenario with a sigmoid response, prescribed levels of effort were very
284 high (0.9), in most of the selected planning units, and quite high (greater than 0.6) in the other
285 planning units selected. In the scenario with a linear response, the highest level of effort was
286 selected in most of the planning units; lower levels of efforts were selected uniformly with
287 very low frequencies among the other planning units. The number of selected planning units
288 for species with convex and linear responses was higher than for species with binary and
289 sigmoid responses.
290
291 3.2. Effect of using species response curves vs. binary responses on the overall cost of threat
292 management: Mitchell River catchment case study
293 The levels of efforts selected in the Mitchell River catchment case study, for the binary
294 scenario (i.e., all species had the same binary response to each action), were distributed in a
295 binary fashion, as a result of the binary response used (Fig. 4a,c). In contrast, selected levels
296 of effort for the continuous-response scenario (i.e., different species had different response
297 curves) ranged from 0 to 1. Most of the selected planning units were prescribed medium to
298 high levels of effort for installation of fish passage devices, and lower levels of effort for
299 riparian fencing (Fig. 4b,d).

300 Accounting for species response curves yielded results that outperformed the use of
301 binary response, as shown in the Mitchell River catchment case study (Fig. 5). For example
302 the cost of achieving the 200 $km^2$ target in the binary scenario (i.e., all species had the same
303 binary response to both action) was 2,295 cost units. The cost of achieving the same target
304 level was 1,835 cost units in the continuous-response scenario (where different species had
305 different response curves for each action) (Fig. 5). This represents a 20 % reduction in the
306 cost of achieving conservation targets relative to the use of binary responses. The magnitude

of the improvement achieved by using our approach was higher for high target levels than for low target levels.

## 4. Discussion

We found that accounting for continuous species responses to varying levels of effort can reduce the overall cost of abating threats to species in systematic conservation planning. Our approach allows more precise allocation of conservation management effort to abate threats to species. This is a key improvement in systematic conservation planning and complementarity-based approaches to threat management, which have assumed that priority actions are always fully implemented (i.e., always equivalent to prescribing the highest level of effort) (Carwardine et al. 2012; Chades et al. 2015; Possingham et al. 2000). Our approach can provide more specific recommendations for on-ground implementation of conservation management actions, thus reducing conservation costs and improving cost-effectiveness of threat management.

### 4.1. Cost of threat management depends on species responses to threats

Incorporating information on the responses of species to actions into systematic conservation planning can improve conservation efficiency (Adams et al. 2014; Carwardine et al. 2012; Wilson et al. 2005). However, no study has demonstrated this by providing a quantitative framework where the response of species to actions depends on continuous levels of management effort allocated to the action. We found that gains in cost-effectiveness depend on the shape of the species response curves. For example, achieving a conservation target for species with convex and sigmoid responses is up to 50% cheaper than achieving species targets using the traditional binary approach (from the results of the simulated example), which assumes that a species response to an action is either 1 or 0 (binary species

response) (as applied by Carwardine et al. 2008; Klein et al. 2008). This is because the conservation target for species with convex and sigmoid responses can be achieved by prescribing lower levels of management effort than in the case of the traditional binary approach. In contrast, the traditional approach always requires an action to be carried out at the highest (fixed) effort possible, thus resulting in higher costs.

The lower level of effort required to achieve targets when using continuous species responses than when using binary responses, translated into 20% lower threat abatement costs, as shown in the case study. The reduction in costs achieved by our approach was smaller in the case study than in the simulated example. This could be due to the fact that the number of species exhibiting convex and sigmoid responses (which are the ones driving the greatest budget savings) was lower in the case study, where we assumed different responses for different species based on species life-history traits, than in the simulated example, where all species had the same type of response to the threat. Ultimately, the extent by which our approach outperforms the traditional binary one depends on how many species with different responses need protection. If the majority of target species exhibits a linear response to the actions, where high conservation gains are achieved at high levels of effort, the improvements in cost-effectiveness of our approach relative to the traditional one might be small.

Our analysis tends to identify priority areas in good conditions, i.e., with a low incidence of threats, because, for a given species response, they are cheaper to act on. This is because our decision problem aims to secure each species over a minimum target proportion of their current spatial distribution; clearly this can be cost-effectively achieved by targeting areas where few threats occur. However, rather than trying to maintain current conditions, an alternative objective would be to improve the benefits gained by implementing an action relative to the benefits gained when no action is implemented (Maron et al. 2013). This type

of analysis would prioritize areas in bad conditions, i.e., with a high incidence of threats, because they might yield higher species benefits when acted upon. Future multi-action prioritization studies should consider this restoration-type of objective as well to aid more cost-effective species restoration (Evans et al. 2015).

Our study suggests that there might be trade-offs between the levels of management effort to allocate to an action, to achieve a target species benefit, and the spatial extent of the area where the effort is prescribed. We found that achieving conservation targets for species with low degrees of vulnerability to a threat (i.e., convex species response) required low levels of management effort spread across a larger area. On the other hand, for more vulnerable species (i.e., sigmoid species response), it was more cost-effective to prescribe higher levels of management effort over a smaller area.

Our findings demonstrate the potential value of improved information on species responses to threats and actions. However, the potential for additional information to improve decision making is constrained by the money and time required to acquire it (Grantham et al. 2009). Acquiring more biological data might fail to improve the cost-effectiveness of conservation planning recommendations particularly in the case of rare species, whose spatial distribution is highly uncertain (Hermoso et al. 2015). Therefore, it is important that future research assesses the trade-offs between the cost of collecting improved information and the gains in cost-effectiveness derived from incorporating that information into a systematic conservation planning framework.

### 4.2. Study limitations

We implemented a novel complementarity-based prioritization approach which accounts for the continuous responses of species to the continuous levels of management effort. However, we have assumed that the maximum benefit achievable for a species in a planning

unit equates the current area of occupancy of the species in a planning unit, which is implicitly linked to a second assumption we made: the species goes locally extinct when no management effort is selected. These assumptions might have overestimated the true benefit of conservation actions, as species conservation value might be different from zero in absence of an intervention (Maron et al. 2013). Nevertheless, our conclusions are unlikely to change if this assumption was to be relaxed, as our aim was to demonstrate the relative effect of different response curve shapes rather than estimating a more accurate benefit of conservation actions (Carwardine et al. 2012; Chades et al. 2015).

We also assumed that the cost of implementing an action in a planning unit increased linearly with the effort allocated to the action. However, for some actions this might not be the case, due to differences in the way different threats respond to management. For instance, the cost per hectare of eradicating introduced herbivores from an area increases as the proportion of the area that is managed increases, since population density declines and individuals are difficult to locate (Bayliss and Yeomans 1989). This suggests that the total cost of eradicating introduced herbivores from a planning unit might increase substantially only after a high level of effort (e.g., hours of aerial shooting) has been applied, and increases exponentially after that (as herbivore density keeps decreasing). Accounting for this 'cost-effort relationship' might increase gains in cost-effectiveness achieved by using species response curves and this issue should be explored further.

Our approach requires detailed input data, including the spatial distribution of species and threats and knowledge of species responses to candidate management actions. While species and threat distribution maps are becoming increasingly available (Guisan et al. 2013; Tulloch et al. 2015), species responses to varying levels of management efforts (for multiple actions) are less likely to be available in many regions due to lack of measurements of local responses of species (Adams et al. 2014). This is why here we assumed the shape of the

response curves of different species to each action. However, an important future step is to test how accurately the assumed curve shapes reflect the true species responses and what is the uncertainty around estimates of species response to management actions (Burgman et al. 2005; McDonald-Madden et al. 2008). Comparative estimates of species responses can be obtained using expert elicitation approaches or field measurements, which are typically resource demanding tasks (money, time, personnel) (Carwardine et al. 2012; Martin et al. 2012; Ng et al. 2014). Here, we used the best available information from the literature to define responses of species to management actions in a robust and easily repeatable way.

### 4.3. Management implications

Our approach has important implications for on-ground priority threat management (Adams et al. 2014; Carwardine et al. 2012; Chades et al. 2015). We are now able to prescribe the specific level of conservation management effort to allocate to conservation management actions, within a complementarity-based planning framework, using information on continuous species responses to actions. For instance, allocating high levels of effort to riparian restoration, as prescribed in some instances by our approach, might correspond to fencing the entire river section of a small planning unit. Similarly, prescribing medium and low levels of effort would consist of fencing 2/3 and 1/3 of the river section in a planning unit, respectively. Furthermore, additional information on the amount of labor required (e.g., hours or/and people needed to fence a specific river section in a planning unit) to implement a specific control action per unit of area, when available, could be used for prioritizing more detailed effort and better guide on-ground management activities.

## 5. Conclusions

We have shown that accounting for continuous species responses to management effort can reduce the cost of threat abatement. We have further demonstrated how to incorporate species response curves into a systematic conservation planning framework, where the complementary contribution of different sites in achieving species benefit is accounted for. While we have demonstrated the use of our approach to the freshwater realm, our method can be applied to the terrestrial and marine realms as well, as long as information on planning units (e.g., management sites, equal-size grid cells, fishing grounds), threats (e.g., habitat loss/degradation, invasive species, fishing), species and species responses are available or can be derived (Auerbach et al. 2014; Mills et al. 2012; Wilson et al. 2011). As conservation budgets become tighter, and the risk of extinction of many species increases, our approach can aid decision makers to optimally allocate conservation management effort, across different realms, to achieve the greatest returns per conservation dollar invested.

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608

609

Table 1. Mathematical functions used to represent different shapes of species response curves.

| Shape | Function |
|---|---|
| Binary | $g_{k,j}(X_{i,k}) = 0$ when $X_{i,k} < 1$<br>$g_{k,j}(X_{i,k}) = 1$ when $X_{i,k} = 1$ |
| Convex | $g_{k,j}(X_{i,k}) = 1 - e^{(a * X_{i,k})}$ |
| Sigmoid | $g_{k,j}(X_{i,k}) = \frac{1}{1 + e^{-b*(X_{i,k} - 0.5)}}$ |
| Linear | $g_{k,j}(X_{i,k}) = X_{i,k}$ |

*Parameters *a* and *b* are constants defined to give the appropriate relationship.

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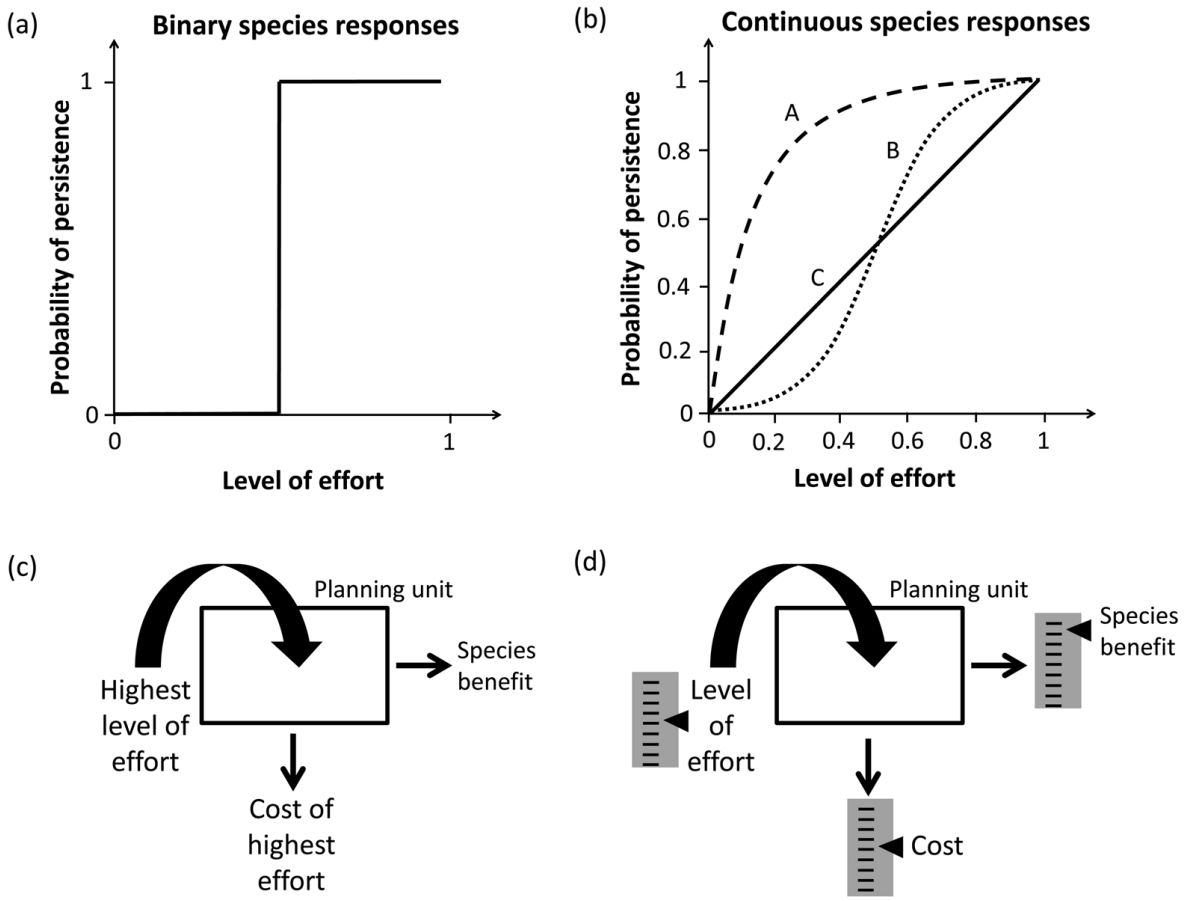
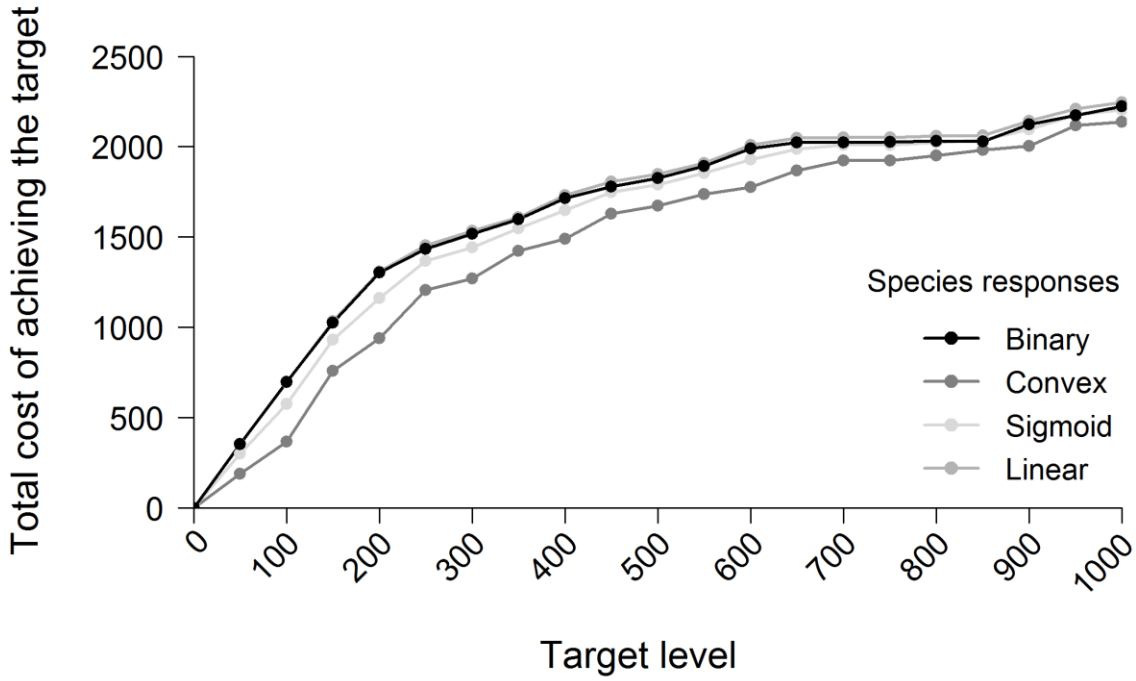
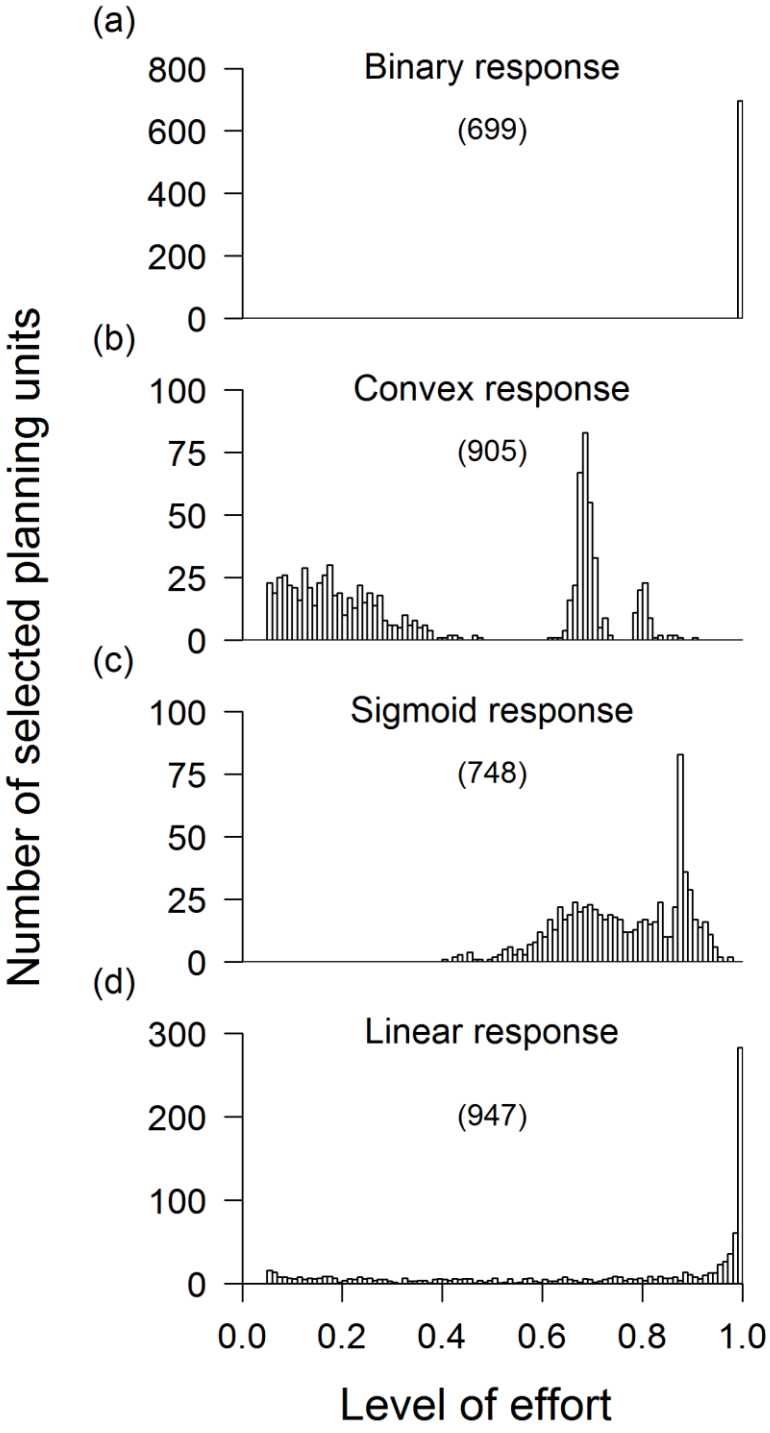



Figure 1. Conceptual framework of the study. The traditional systematic conservation planning approach is based on a binary species response (a), which assumes that (1) an action is either not implemented or fully implemented through allocation of the highest level of effort; and (2) when the action is not implemented, the probability of persistence of a species in a planning unit is 0; when the action is implemented, the probability of persistence of a species in a planning unit is 1. As a consequence, the cost of implementing an action in a planning unit corresponds to the cost of selecting the highest level of effort of an action (c). However, when the species response is represented using a continuous curve of varying shapes (b) such as convex (A), sigmoid (B) or linear (C), any level of effort can be prescribed, with continuous species benefits. In this case, the cost of implementing the action in a planning unit depends on the level of effort selected to achieve a target probability of persistence (d).



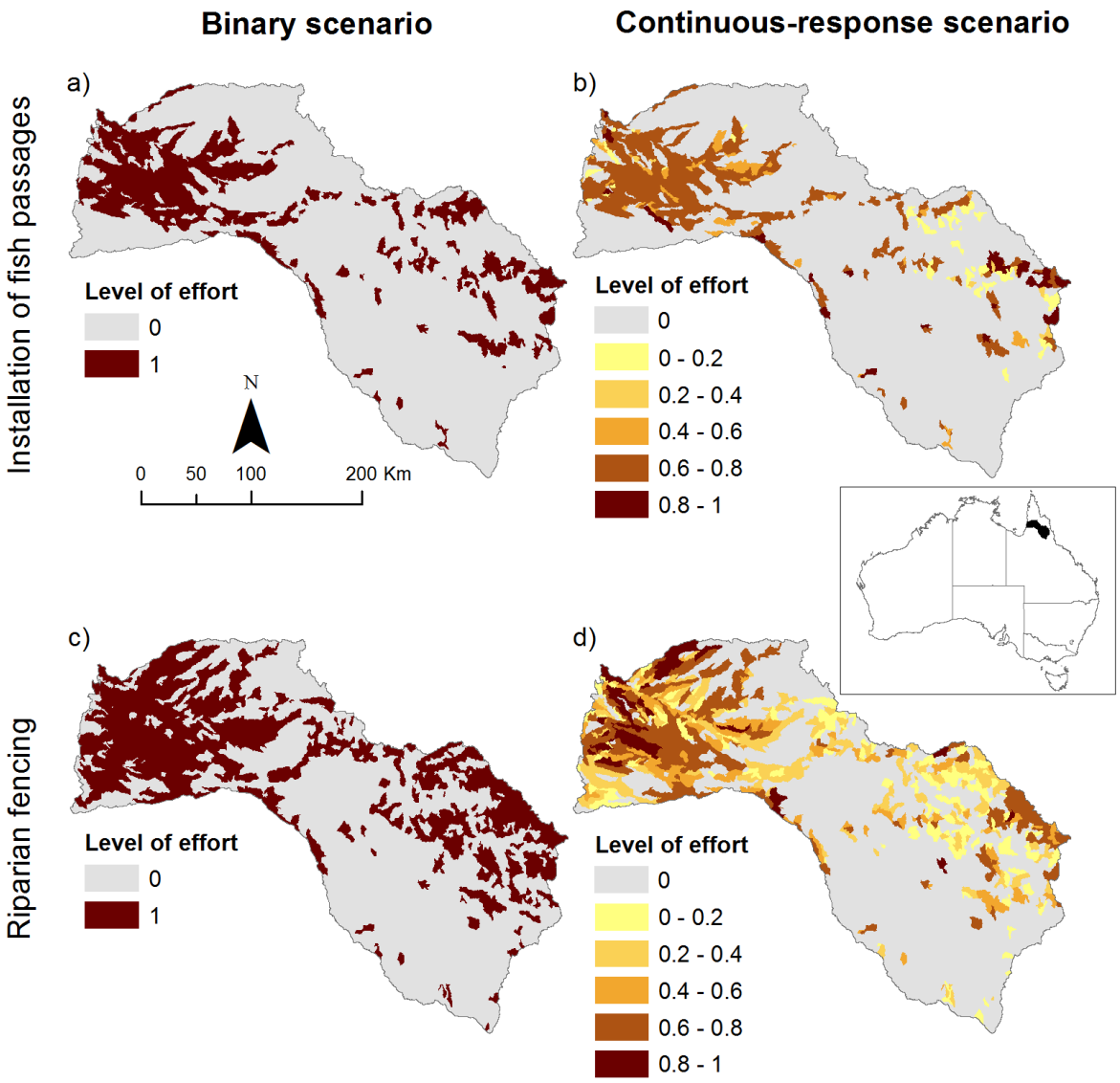

624

625 Figure 2. Total cost of achieving the species targets as the target level increases, for different
626 shapes of species response curves (Binary, Convex, Sigmoid and Linear), as calculated in the
627 simulated example. The target level refers to the area ($km^2$) where each species has a
628 probability of persistence of 1. Results shown are from the 'best' solution (the one with
629 lowest value of the objective function) of 10 replicate prioritization runs of each combination
630 of species response and target level.




631

632 Figure 3. Histograms of the levels of effort prescribed in selected planning units, for different
633 shapes of species response curves (Binary, Convex, Linear and Sigmoid), in the simulated
634 example. Numbers in parentheses indicate the total number of selected planning unit for each
635 response scenario. Results are shown for a fixed target level (i.e., probability of persistence of
636 1 across 100 $km^2$).




637

638 Figure 4. Spatial distribution of selected level of effort for installation of fish passage devices
639 on dams, weirs and other barriers (a, b) and fencing of riparian vegetation (c, d) and two
640 scenarios ('binary' and 'continuous-response'), as output from the Mitchell River catchment
641 case study. In the 'binary' scenario (a, c) all species had the same binary response to each of
642 the two actions; in the 'continuous-response' scenario (b, d) different species had different
643 response curves for different actions. Each scenario corresponded to a separate run of the
644 simulated annealing algorithm. Results are shown for a fixed target level (i.e., probability of
645 persistence of 1 across 100 $km^2$). The inset map shows the case study area.

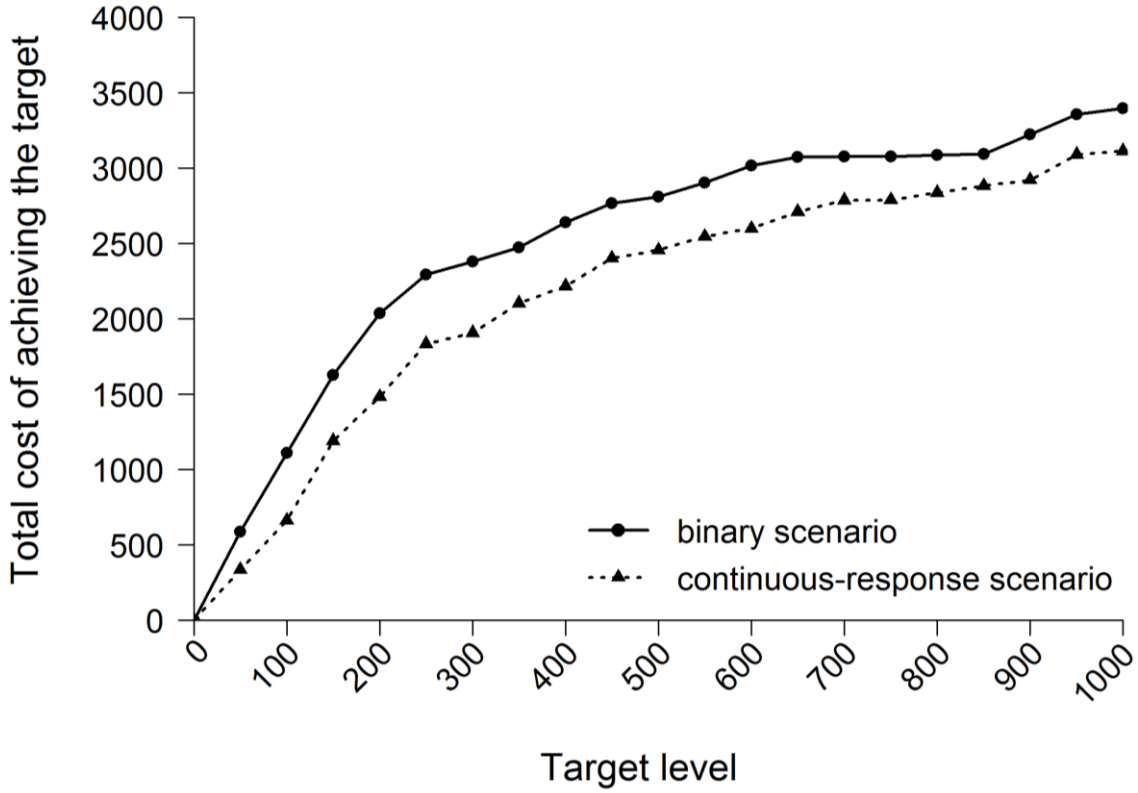



Figure 5. Total cost of achieving the species targets as the target level increases, for different threat management scenarios, as quantified in the Mitchell River catchment case study. In the 'binary' scenario all species had the same binary response to each action (i.e., binary effort and binary outcome); in the 'continuous-response' scenario different species had different response curves for different actions. The target level refers to the area ($km^2$) where each species has a probability of persistence of 1. Results shown are from the 'best' solution (the one with lowest value of the objective function) of 10 replicate prioritization runs of each combination of species response and target level.

**Appendix S1.** Simulated annealing algorithm**.**

**Appendix S2.** Mitchell River catchment case study: Freshwater fish species responses to actions.